A Mechanistic Approach to Evaluation of Umbrella Species as Conservation Surrogates

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Abstract: *Although species with large area requirements are sometimes used as umbrella species, their general utility as conservation tools is uncertain. We surveyed the species diversity of birds, butterflies, carabids, and forest-floor plants in forest sites across an area (1600 km²) in which we delineated large breeding home ranges of Northern Goshawk (*Accipiter gentilis*). We tested whether protection of the home ranges could serve as an effective umbrella to protect sympatric species of the four taxa. We also used an empirical habitat model of occupancy of home range to examine mechanisms by which the Northern Goshawk acts as an umbrella species. Among species richness, abundance, and species composition of the four taxa, only abundance and species composition of birds differed between sites located inside and outside home ranges, which was due to greater abundance of bird species that were prey of Northern Goshawks inside the home ranges. Thus, although home range indicated areas with high abundance of certain bird prey species, it was not effective as an indicator of the species diversity of all four taxa. We also did not find any difference in species richness, abundance, and species composition between sites predicted as occupied and unoccupied using the habitat model. In contrast, when we selected sites on the basis of each habitat variable in the model, habitat variables that selected sites either in agricultural or forested landscapes encompassed sites with high species richness or particular species composition. This result suggests that the low performance of the Northern Goshawk as an umbrella species is due to this species' preference for habitat in both agricultural and forested landscapes. Species that can adjust to changes in habitat conditions may not act as effective umbrella species despite having large home ranges.*

Keywords: *Accipiter gentilis*, biodiversity, habitat model, home range, indicator species, Japan, Northern Goshawk

Un Método Mecanicista para la Evaluación de Especies Sombrilla como Substitutos de Conservación

Resumen: *Aunque las especies con territorios grandes son utilizadas ocasionalmente como especies sombrilla, su utilidad general como herramientas de conservación es incierta. Muestreamos la diversidad de especies de aves, mariposas, carábidos, y plantas en sitios forestales en un área (1600 km²) en la que delineamos los rangos de hogar reproductivo de* Accipiter gentilis. *Probamos si la protección de los rangois de hogar puede fungir como una sombrilla efectiva para proteger especies simpátricas de cuatro taxa. También utilizamos un modelo empírico de la ocupación del rango de hogar para examinar mecanismos mediante los cuales* A. gentilis *actúa como una especie sombrilla. Entre la riqueza, abundancia y composición de especies de los cuatro taxa, solo fueron diferentes la abundancia y composición de especies de aves en sitios dentro y fuera de los rangos de hogar, lo que se debió a la mayor abundancia de especies de aves que eran presas de* A. gentilis *dentro de los rangos de hogar. Por lo tanto, aunque el rango de hogar indicaba áreas con abundancia alta de ciertas especies de aves presas, no fue efectivo como un indicador de la diversidad de especies de los cuatro taxa. Tampoco encontramos diferencias en la riqueza y abundancia de especies ni en la composición de especies entre sitios pronosticados como ocupados y no ocupados mediante el modelo de hábitat. En contraste, ciando seleccionamos sitios basados en cada variable de hábitat en el modelo, las variables de hábitat que*

seleccionaron sitios en paisajes agrícolas o forestales abarcaron sitios con riqueza de especies alta o con una composición de especies particular. Este resultado sugiere que el pobre rendimiento de A. gentilis *como una especie sombrilla se debe a que su preferencia de hábitat tanto en paisajes agrícolas como forestales. Es posible que las especies que se pueden ajustar a cambios en las condiciones del hábitat no funjan efectivamente como especies sombrilla a pesar de tener rangos de hogar extensos.*

Palabras Clave: *Accipiter gentilis*, biodiversidad, especie indicadora, Japón, modelo de habitat, rango de hogar

Introduction

Monitoring and assessing biodiversity of whole biota is extremely time consuming and costly because there are so many species in an area (Gaston 1996; Oliver & Beattie 1996; Lawton et al. 1998). Thus, conservation biologists have showed growing interest in developing proxies that will offer practical shortcuts for management of biodiversity (Howard et al. 1998; Noss 1999; Margules & Pressey 2000). An umbrella species is one such proxy (Landres et al. 1988; McGeoch 1998; Caro & O'Doherty 1999). We define an *umbrella species* as a species with large area requirements for which protection of the species offers protection to other species that share the same habitat (Noss 1990; Simberloff 1998). Thus, protecting an umbrella species should theoretically save an entire suite of sympatric species with similar habitat requirements (Simberloff 1999). However, for an umbrella species to function effectively, the area selected for protection under an umbrella species approach should more efficiently protect other species than an equivalent area not selected using such an approach (Suter et al. 2002; Caro 2003; Caro et al. 2004) or selected on the basis of random procedures (Andelman & Fagan 2000; Fleishman et al. 2001). The effectiveness of the umbrella species approach, which relies on significant overlap between habitat requirements for umbrella species and sympatric species, rarely has been evaluated however (Carroll et al. 2001).

Umbrella species differ from other biodiversity indicators in that they are used to specify not only the type of habitat but also the size of the area to be protected (Caro & O'Doherty 1999). Because large predators have large home ranges, their habitat requirements may encompass those of many other species (Wallis de Vries 1995; Noss et al. 1996). Thus, umbrella species are often high-trophic-level mammalian or avian predators (Wilcox 1984; Landres et al. 1988). However, most researchers who have evaluated the umbrella species concept examined only whether the presence or absence of the umbrella species could serve as a proxy for the presence or absence of sympatric species (e.g., Ryti 1992; Launer & Murphy 1994; Martikainen et al. 1998; Chase et al. 2000; Rubinoff 2001). Although these researchers did not evaluate the size of the area identified by an umbrella species approach, they persisted in using the umbrella species

virtually synonymously with biodiversity indicators (Caro 2003).

In contrast, Berger (1997) and Caro (2001, 2003) examined whether an area that is sufficiently large to protect a viable population of an umbrella species is also able to protect viable populations of sympatric species. But they did not evaluate the type of habitat used by the population of umbrella species. We overcame this problem by examining whether large breeding home ranges of a raptor, the Northern Goshawk (*Accipiter gentilis*), can serve as an effective umbrella to protect sympatric species. We used home range instead of presence/absence measures because it allows evaluation of the usefulness of umbrella species at the particular scale for which management of the umbrella species should be considered (Caro 2003).

Another limitation of previous studies is that they poorly identified the mechanism by which an umbrella species concept is successful in protecting sympatric species because they have been based primarily on the overlap of species distributions (Roberge & Angelstam 2004). Results of a few studies show that species with habitat requirements similar to those of an umbrella species would be protected by conserving the umbrella species (Suter et al. 2002; Pakkala et al. 2003). However, researchers did not quantify habitat requirements of the umbrella species by modeling their habitat suitability. Only Carroll et al. (2001) developed habitat models of proposed umbrella species, but they did not evaluate whether these species act as effective umbrella species. We used here an empirical habitat model that estimates the probability for Northern Goshawks occupying their home ranges, and investigated whether the predicted occupied areas can serve as an effective umbrella to protect sympatric species. Using the habitat model, we partitioned Northern Goshawk habitat requirements into each habitat variable in the model and examined mechanisms by which the Northern Goshawk acts as an umbrella species.

The Northern Goshawk is regarded as an umbrella species of the rural landscape of Japan (Sato & Niisato 2003), which consists of a mosaic of patches of forests, arable lands, and grasslands and harbors species-rich fauna and flora. These rural landscapes have been lost or have deteriorated over the last few decades, leading to a rapid biodiversity loss in Japan (Washitani 2001).

The Northern Goshawk, which is legally protected under the Law for the Conservation of Endangered Species of Wild Fauna and Flora in Japan, is used to prioritize conservation areas in these landscapes because it is the top predator and has greater area requirements than any other animals living in this landscape. In the United States, the Northern Goshawk is used as a management indicator species in many national forests to assess the impacts of forest management procedures on their populations and the populations of other species with similar habitat requirements (Graham et al. 1999; Drennan & Beier 2003). However, the umbrella function of this species has never been tested in Japan or in the United States. We surveyed species diversity of birds, butterflies, carabids, and forest-floor plants in a number of forest sites to evaluate whether the sites selected by the umbrella species approach are efficient in protecting species diversity of the four taxa.

Methods

Study Area

We examined a 1600-km^2 area in the Ishikari region, central Hokkaido, northern Japan (43° 10'N, 141° 30'E). The elevation ranges from 0 to 800 m. Average monthly temperatures in this area are between $-6°$ C and 23° C with an annual precipitation of 1000 mm. Topographically, most of the area is situated on a lowland plain bordered by low mountains to the northwest and southwest of the study area. These mountains were primarily covered with cool–temperate mixed forests dominated by Sachalin fir (*Abies sachalinensis* Masters), painted maple (*Acer pictum* Thunb.), Japanese elm (*Ulmus davidiana* var. *japonica* Nakai), mizunara oak (*Quercus crispula* Blume), and Japanese white birch (*Betula platyphylla* var. *japonica* Hara). These forests naturally regenerated after logging within the past 100 years. Conifer plantations of Japanese larch (*Larix kaempferi* Carriere) and Sachalin fir are also present.

The southwestern part of the lowland plain is occupied by the city of Sapporo with a population of 1,700,000. The rest of the lowland plain mainly consists of an agricultural landscape with a mosaic of arable fields and forest fragments. Natural forests in the lowland plain contain tree species similar to those in the surrounding mountains, but plantation forests, most of which were established >40 years ago, consist of Manchurian ash (*Fraxinus mandshurica* Rupr.), Japanese larch, Norway spruce (*Picea abies* Karsten), and Sachalin spruce (*Picea glehnii* Masters).

Home Range and Habitat Model

Detailed descriptions of home range delineation and habitat modeling are in Kudo et al. (2005). We identified breeding home ranges of 36 male goshawks through a system-

atic nest survey and extensive radiotelemetry tracking between 1998 and 2002. Then, we sampled 44 unoccupied plots of 2-km radius that were similar in size to the average home range in the study area. We determined values of habitat variables (forest land cover, open [arable fields, abandoned fields], water, and urban) within each home range and unoccupied plot with a land-cover map. We also obtained the mean and the mode of slopes (in degrees) from a 50-m grid, digital elevation model. We compared these habitat variables between the home ranges and unoccupied plots with a stepwise logistic regression, which yielded the following multivariate model that estimated the probability of Northern Goshawk use of each home range and the probability that a plot would be unoccupied (classification accuracy = 84%).

$$\ln(p/1 - p) = -2.822 + 0.119x_1 + 0.087x_2 \\ -0.272x_3 - 0.747x_4, \tag{1}$$

where p is the probability of occupancy, x_1 is the proportion of forest >200 m from the forest edge (defined as the proportion of forest interior), x_2 is the proportion of open land <200 m from the forest edge (defined as the proportion of open land near forests), x_3 is the proportion of water, and x_4 is the mode of slope (defined as the slope).

Species Diversity Surveys

We conducted species diversity surveys during 1999–2001 at 44 study sites in forests located across the study area. We did not sample sites from urban areas because Northern Goshawks do not nest in urban areas (Kudo et al. 2005). To reduce site effects, we selected forest sites with relatively similar conditions: all sites were in secondary forests >40 years old with closed canopy, which are used by Northern Goshawks for foraging.

For the bird surveys, we walked along a 1-km census route for 1 hour at each site during the breeding season (3–26 June). We recorded all birds seen or heard within 25 m of either side of the routes but did not record birds seen flying above the canopy. We completed the surveys in morning (0400–0900 hours) on fine days when birds were most active.

For butterfly counts, we walked a 1-km census route for 1 hour every week at each site during the adult flight season (early June–early September; 13 surveys in 1 year) (Ozaki et al. 2004). The census routes were similar to the routes used in the bird survey. We recorded all butterflies within 5 m of either side of and 5 m above the routes. We collected species that were not clearly distinguishable in flight for identification. We completed the surveys between 0900 and 1500 hours on fine days when weather conditions were suitable for butterfly activity.

We used a line of 10 pitfall traps (200-mL plastic cups, 65 mm in diameter) spaced at 1-m intervals to sample carabids at each site. We set traps in early June, late July,

and early September, and left them there for 2 weeks. This time frame encompassed the activity peak of carabids in the study area (M. I., unpublished data). We used 40 mL of 20% acetic acid solution as a preservative in each trap.

For forest-floor plants, we set a 50×10 m transect in each site. We then divided the transect into 20 5×5 m sections and set a 1×1 m subquadrat at the center of every sections. We recorded all the vascular plants <2 m in height in the subquadrats.

Surrogate Schemes

We selected sites inside the home ranges of the 36 male goshawks for the scheme on the basis of home ranges. For the scheme based on predicted occupancy, we estimated the probability of occupancy in each site from the habitat model (Eq. 1). We calculated the four habitat variables in the model from the area within a 2-km radius around each site because this area was similar to the average home range size. We classified sites as being occupied when the estimated probability of occupancy was >0.5 (Kudo et al. 2005). Finally, we selected sites suitable as Northern Goshawk habitat in terms of each habitat variable in the model. When the habitat variables were positively associated with the probability of occupancy in the model (i.e., the proportion of forest interior and the proportion of open land near forests), we selected sites in descending order starting with the highest value for the habitat variables. When the habitat variables were negatively associated with the probability of occupancy in the model (i.e., the proportion of water and the slope), we selected sites in ascending order starting with the lowest value for the habitat variables. In these schemes, we selected the same number of sites as in those based on home ranges because comparing schemes with equal numbers of selected sites ensured the same statistical power; thus, varying results would be due to the difference in schemes rather than differences in the number of sites selected.

Evaluating Effectiveness of Surrogate Schemes

For analyses of species diversity, we excluded the Northern Goshawk from bird species and assigned the remaining bird species to prey or nonprey of Northern Goshawks (Anonymous 2003). For butterflies and carabids, we combined abundances of each species found throughout the survey period. We excluded exotic species of forest-floor plants and estimated plant abundance as the number of subquadrats in which we detected the species. No exotic species were recorded from the other three taxa. We used Mann–Whitney tests to determine whether species richness or abundance of each taxon differed between selected sites and unselected sites in each scheme. The number of rare species, which we defined here as those detected at <4 sites, were also compared between selected and unselected sites.

We then compared species composition of each taxon between selected and unselected sites with multiresponse permutation procedures (MRPPs). An MRPP is a nonparametric procedure for testing the hypothesis of no difference in species composition between two or more groups at the community level (McCune & Grace 2002). It uses the average within-group distance to summarize the observed pattern of dissimilarities among the groups and tests whether the distance is smaller than expected by chance through permutation procedures. In MRPP chance-corrected within-group agreement, A, describes within-group homogeneity compared with the random expectation. We used rank-transformed Sorensen distance to make the analysis analogous to nonmetric multidimensional scaling. Prior to the analyses, we transformed the abundance of each species of birds, butterflies, and carabids to the square root because this provided the minimum stress when we applied nonmetric multidimensional scaling to these taxa.

We then performed indicator species analysis (Dufrêne & Legendre 1997) on the species detected at >3 sites to compare species composition at the species level. For each species, we calculated an indicator value that was the product of a relative abundance (the proportion of abundance of a species in a group relative to the abundance of that species in all groups) and a relative frequency (the proportion of sites that contained that species in each group). Because an indicator value combines information on the exclusiveness of species abundance and the faithfulness of species occurrence in a single group, it is a better index than abundance to identify species that are responsible for the difference in species composition between groups. Each indicator value was tested using a Monte Carlo test with 1000 randomizations. The MRPP and the indicator species analysis were performed with PC-Ord (version 4.25; McCune & Mefford 1999).

For the statistical tests, we set alpha = 0.05 for each comparison. We did not use any methods of multiple comparison to adjust the table-wide Type I error rate, because these procedures are too conservative and inflate the cost of not detecting real differences in each comparison (Type II errors) (Moran 2003; Roback & Askins 2005).

Results

We detected 51 bird species other than the Northern Goshawk, 72 butterfly species, 64 carabid species, and 262 native forest-floor plant species. Of the 51 bird species, 19 were prey of Northern Goshawks. (A list of prey and nonprey species recorded is available from K.O.) Among 44 study sites, 22 were inside the home ranges and 21 were predicted as occupied. Only 12 out of 22

sites inside the home ranges were predicted as occupied. Among the surrogate schemes based on habitat variables, the sites selected on the basis of the slope overlapped to a large degree (15 out of 22) with the sites selected on the basis of the proportion of open land near forests. These two schemes selected sites in agricultural landscapes in the lowland plain. Sites selected by these variables were different from sites selected by the proportion of forest interior mostly because this scheme selected sites in forested landscapes where large forest patches have been retained. Only 2 out of 22 sites selected by the slope were also selected by the proportion of forest interior, and 8 out of 22 sites selected by the proportion of open land near forests were also selected by the proportion of forest interior. Sites selected on the basis of the proportion of water overlapped moderately (9–12 out of 22) with sites selected by other habitat variables.

Species Richness and Abundance

In the scheme based on home ranges, species richness did not differ between selected and unselected sites in any taxon (Table 1). Only bird abundance was greater (49%) in selected sites than in unselected sites because of the 82% greater abundance of bird prey species in selected sites. Abundance of nonprey species did not differ between selected and unselected sites (Mann–Whitney test, $U = 193$, $p = 0.253$). The numbers of rare species were never greater in selected sites than in unselected sites, although the number of rare bird species was greater in unselected sites than in selected sites. The scheme based on predicted occupancy did not perform better than the home range scheme. Neither species richness, abundance, nor the number of rare species in any taxon differed between selected and unselected sites.

In contrast, some habitat variables provided better schemes for selection of sites with high species richness or high abundance than home ranges or predicted occupancy (Table 1). When selecting sites on the basis of the slope, those selected had 26% greater species richness of bird prey species, 31% greater species richness of carabids, 52% greater abundance of all birds, and 2.1 times greater abundance of bird prey species than unselected sites. Abundance of bird prey species was also 53% greater in sites selected on the basis of the proportion of open land near forests. In contrast, the scheme based on the proportion of forest interior selected sites that had 21% greater species richness of all birds, 2.7 times greater number of rare bird species, 31% greater species richness of all butterflies, and 2.9 times more rare butterfly species than unselected sites. These taxa differed from the taxa with higher species richness in the schemes based on slope or on the proportion of open land near forests. However, sites selected on the basis of the proportion of water were not any different in species richness, abundance, and the number of rare species from unselected sites.

Species Composition

We evaluated 34 bird species, 46 butterfly species, 40 carabid species, and 88 native forest-floor plant species in the indicator value analysis. Birds were the only taxon that had different species composition between selected and unselected sites in the scheme based on home ranges (Table 2). Monte Carlo test showed that four bird species, all of which were prey of Northern Goshawks, and one plant species had higher indicator values in selected sites than expected by chance (Fig. 1). In the scheme based on predicted occupancy, species composition did not differ between selected and unselected sites in any taxon. Only two bird species and two butterfly species had significantly higher indicator values in selected sites. These two bird species were also prey of Northern Goshawks but were different from the species with higher indicator values in the home range scheme.

In contrast to the low performance of these schemes, the schemes based on some of the habitat variables encompassed sites with particular species composition. For example, differences in species composition were highly significant ($p < 0.0001$) in every taxa when we selected sites based on the slope. Thirty-six (17.3%) out of 208 species tested in indicator species analyses had significantly higher indicator values in selected sites. Species composition also differed in birds, butterflies, and carabids when we selected sites based on the proportion of open land near forests. In this scheme, 14 species (6.7%) had higher indicator values in selected sites, and 12 of them overlapped with the species with higher indicator values in the scheme based on the slope. When we selected sites based on the proportion of forest interior, differences in species composition were also highly significant ($p < 0.0001$) in every taxa. In this scheme, 37 species (17.8%) had higher indicator values in selected sites, and none of them overlapped with the species with higher indicator values in the schemes based on slope or proportion of open land near forests. Finally, when we selected sites based on the proportion of water, species composition differed only in butterflies, with only four species having higher indicator values in selected sites.

Discussion

Our results revealed that among the four taxa, only bird abundance was significantly greater in selected sites than in unselected sites in the home-rage scheme. Bird species composition also differed between selected and unselected sites, but indicator species analyses showed only four bird species that had significantly higher indicator values in selected sites than expected by chance. The results were even worse when we selected sites based on predicted occupancy because we did not find any difference between selected and unselected sites in

Table 1. Comparison of species richness, abundance, and the number of rare species of each taxon between sites selected and not selected by six surrogate schemes.[a]

| | | Surrogate scheme | | | | | | | | | | | | | | | | | |
| | | home range | | | predicted occupancy | | | slope | | | proportion of open land near forests | | | proportion of forest interior | | | proportion of water | | |
Taxon	Measurement	select	unsel	p	select	unsel	p	select	unsel	p	select	unsel	p	select	unsel	p	select	unsel	p
Bird																			
all species	species richness	11.8	11.7	0.841	11.1	12.4	0.133	11.0	12.6	0.089	10.9	12.7	0.023	12.9	10.6	0.015	12.5	11.1	0.113
	abundance	49.9	33.5	0.049	45.7	38.1	0.335	50.3	33.1	0.008	46.2	37.2	0.213	34.8	48.6	0.098	46.7	36.7	0.053
	no. rare species	0.4	0.8	0.045	0.4	0.8	0.081	0.4	0.8	0.077	0.4	0.8	0.132	0.9	0.3	0.024	0.7	0.5	0.214
prey species[b]	species richness	7.6	6.5	0.060	7.0	7.1	0.584	7.9	6.2	0.007	7.3	6.8	0.568	6.2	7.9	0.007	7.2	6.9	0.651
	abundance	43.4	23.9	0.013	38.5	29.2	0.235	45.9	21.4	<0.001	40.7	26.5	0.009	22.5	44.7	0.001	37.1	30.2	0.366
Butterfly	species richness	19.9	22.0	0.186	20.2	21.6	0.321	18.7	23.1	0.003	20.1	21.7	0.233	23.7	18.1	<0.001	20.7	21.1	0.741
	abundance	288.3	312.8	0.690	312.4	289.7	0.716	269.4	331.7	0.445	264.1	337.0	0.330	333.7	267.4	0.296	341.1	260.0	0.280
	no. rare species	0.7	1.3	0.065	0.8	1.2	0.245	0.6	1.3	0.030	0.7	1.2	0.221	1.5	0.5	0.009	1.1	0.9	0.592
Carabid	species richness	14.2	12.7	0.323	13.2	13.7	0.654	15.3	11.7	0.025	13.7	13.3	0.897	10.9	16.1	<0.001	13.2	13.8	0.796
	abundance	295.4	208.3	0.622	240.7	262.0	0.155	270.5	233.2	0.805	231.6	272.0	0.076	226.3	277.4	0.716	281.9	221.8	0.673
	no. rare species	1.0	0.9	0.500	1.0	1.0	0.680	1.2	0.7	0.076	0.9	1.0	0.417	0.5	1.4	0.029	1.1	0.8	0.355
Native forest-floor plant	species richness	25.1	24.2	0.897	21.8	27.3	0.135	19.8	29.5	0.008	20.8	28.5	0.084	27.0	22.3	0.231	25.4	23.9	0.944
	abundance	108.8	96.8	0.270	95.6	109.4	0.312	86.1	119.5	0.054	91.9	113.7	0.336	110.5	95.1	0.511	109.0	96.6	0.925
	no. rare species	6.7	6.1	0.515	5.7	7.0	0.265	5.7	7.1	0.554	5.4	7.4	0.375	6.4	6.4	0.546	7.3	5.5	0.470

[a] *Mean values for selected (select) and unselected (unsel) sites. Probability values from Mann–Whitney tests.*
[b] *Bird species recorded as prey of Northern Goshawks.*

Table 2. Results of multiresponse permutation procedures (MRPP) comparing species composition of each taxon between sites selected and not selected by six surrogate schemes.*

	Surrogate scheme					
Taxon	*home range* A (p)	*predicted occupancy* A (p)	*slope* A (p)	*proportion of open land near forests* A (p)	*proportion of forest interior* A (p)	*proportion of water* A (p)
Bird	0.049 (0.010)	0.016 (0.140)	0.243 (<0.001)	0.086 (<0.001)	0.219 (<0.001)	0.018 (0.126)
Butterfly	0.019 (0.095)	0.004 (0.321)	0.181 (<0.001)	0.087 (<0.001)	0.173 (<0.001)	0.035 (0.024)
Carabid	0.008 (0.245)	0.011 (0.201)	0.273 (<0.001)	0.084 (0.001)	0.267 (<0.001)	0.008 (0.241)
Native forest-floor plant	0.006 (0.259)	0.011 (0.186)	0.102 (<0.001)	0.018 (0.096)	0.098 (<0.001)	0.008 (0.233)

**Chance-corrected within-group agreement, A, describes within-group homogeneity compared with the random expectation.*

species richness, abundance, or species composition in any taxon. In contrast, the schemes based on several habitat variables encompassed sites with high species richness or particular species composition, suggesting that Northern Goshawk home range and predicted occupancy are not suitable as effective indicators of the species diversity of the four taxa.

Among the schemes based on habitat variables, the scheme based on the slope and the scheme based on the proportion of open land near forests selected mostly similar sites, which were located in agricultural landscapes. Association between slope and species diversity was probably because the scheme based on the slope selected sites in agricultural landscapes. In contrast, the scheme based on the proportion of forest interior selected sites in forested landscapes. These findings suggest that if one were to choose a particular landscape type at the scale of Northern Goshawk home range, it could be an effective indicator of high species richness or particular species composition in some taxa. However, although Northern Goshawks are sensitive to habi-

tat features when establishing home ranges, Northern Goshawks locate home ranges both in agricultural and forested landscapes, and the proportion of forest cover in each home range varied widely between 2 and 88% (Kudo et al. 2005).

Northern Goshawks forage mainly in forest interiors (Finn et al. 2002) or in large forest patches (Widen 1989) in forested landscapes, whereas they use forest edge as cover and take prey by surprise attack in open, agricultural landscapes (Kenward 1982). Thus, Northern Goshawks may adjust to landscape changes by shifting their foraging sites within home ranges. Because of the use of different landscape types, Northern Goshawk home ranges or predicted occupancy do not specify a single type of habitat to be protected, which may explain the low performance of the Northern Goshawk as an umbrella species. This emphasizes the difficulty of using large predators as umbrella species if the predators are habitat generalists that easily adjust to changes in environmental conditions by shifting their foraging sites and consequently do not select sites based on biodiversity values (e.g., Noss et al. 1996; Kerr 1997; Simberloff 1998; Linnell et al. 2000). In contrast, a consistent association between sites occupied by five raptor species and high biodiversity occurs when the raptors have specialized habitat requirements (Sergio et al. 2005).

Home ranges were associated with a higher abundance of bird prey species, which were the main prey items for Northern Goshawks in the study area. Specifically, four bird species that had higher indicator values inside the home ranges were all prey species. These results suggest that Northern Goshawk home ranges can indicate areas with high abundance of bird prey species. Previous studies of habitat selection also suggest that prey abundance is an important factor when Northern Goshawks choose where to locate their home ranges within a larger landscape (Reynolds et al. 1992; Beier & Drennan 1997; Drennan & Beier 2003). However, their prey species vary among subpopulations (Cramp & Simmons 1980; Widen 1997), and this variation in prey species likely reflects differences in the composition, abundance, and availability of birds in their foraging sites (Reynolds et al. 1992). Thus, one should specify what bird species are prey upon
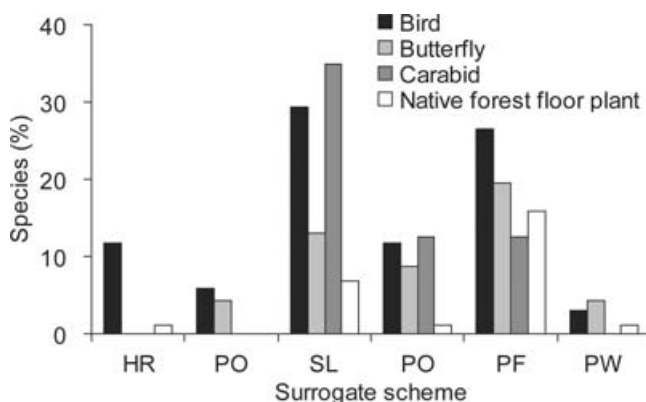

Figure 1. Percentage of species with significantly higher indicator values in sites selected by six surrogate schemes. Surrogate scheme abbreviations: HR, home range; PO, predicted occupancy; SL, mode of slope; PO, proportion of open land near forests; PF, proportion of forest interior; PW, proportion of water.

in an area before using home range as an indicator of bird diversity.

We found no evidence to support the claim that Northern Goshawks are effective indicators of the species diversity of butterflies, carabids, or forest-floor plants. Large raptors are often considered good indicators of whole biodiversity because they are top predators (Rodríguez-Estrella et al. 1998). However, our results suggest that even if Northern Goshawks are indicative of the abundance of their prey, they do not represent the diversity of the other members of the food web. Most of the studies that provide evidence of the effectiveness of the umbrella species examined only the congruence within taxa (e.g., Caro 2001; Ranius 2002; Caro 2003), although there have been some exceptions (Swengel & Swengel 1999; Betrus et al. 2005). For example, Suter et al. (2002) found high species richness and abundance of mountain birds in plots with Capercaillie (*Tetrao urogallus*) and suggested that Capercaillie may also be an umbrella species for invertebrates. However, our results suggest that effectiveness of an umbrella species within taxa does not always confer effective protection for species in different taxa.

In contrast to our results, Northern Goshawks are effective biodiversity indicators in the Italian Alps, where their main habitat is mature forests (Sergio et al. 2005). Thus, usefulness as an umbrella species differs between subpopulations within a same species. This emphasizes the importance of the mechanistic approach to evaluate the general utility of umbrella species as a conservation tool. In this respect, post hoc selection of charismatic species or legally protected species is unlikely to identify effective umbrella species. Our results also indicate that species sensitive to habitat features such as the proportion, size, and configuration of each landscape element can be effective indicators of species diversity. Therefore, prospective and systematic selection of those species (Lambeck 1997; Fleishman et al. 2000, 2001; Betrus et al. 2005) based on habitat of biodiversity concern may be useful in choosing an effective umbrella species.

In Japan, Northern Goshawks inhabit human-dominated rural landscapes that have been intensively used for agriculture and forestry, where protected areas are usually restricted to small areas within these landscapes. However, to maintain viable populations of Northern Goshawks, conservation-minded management of large areas is needed. These large areas may also serve to protect many other sympatric species inhabiting rural landscapes. As a flagship species, Northern Goshawks raise conservation awareness and help promote expenditure on biodiversity conservation (Caro et al. 2004) in rural landscapes. In these respects, protection of Northern Goshawks may confer benefits on sympatric species, although there is little reason to believe that areas protected for Northern Goshawks will be effective in conserving sympatric species in our study area.

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